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Entyloma eranthidis sp. nov. on *Eranthis longistipitata* from Uzbekistan

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Abstract—A new smut fungus, *Entyloma eranthidis* on *Eranthis longistipitata* from Uzbekistan, revealed by molecular, morphological, and ecological evidence, is described and illustrated. It differs from all other species of *Entyloma* by host specialization on *Eranthis* and by having longer (≤35(–38) µm) spores and thicker (≤10(–12) µm) spore walls. ITS rDNA sequence analysis indicates that the new species does not cluster with other species of *Entyloma* on *Ranunculaceae.*

Key words—*Entylomataceae,* phylogeny, taxonomy

Introduction

Eranthis Salisb. (*Ranunculaceae*) is a small genus with a geographic range extending from southern Europe and Turkey to central and east Asia. It contains eleven species (Rukšāns & Zetterlund 2018, Park & al. 2019). Four are with yellow perianth-segments: *E. hyemalis* (L.) Salisb. (native to South Europe), *E. cilicica* Schott & Kotschy (in the Taurus Mts and Iranian and Iraq Kurdistan; considered by some authors conspecific with previously named species; Davis & al. 1965, Tutin 1993), *E. iranica* Rukšāns & Zetterl. (from Iran), and *E. longistipitata* Regel (from central Asia) (Frizen 1993, Rukšāns & Zetterlund 2018, Park & al. 2019). The remaining species produce white

perianth-segments and have a limited distribution in the Altai-Sayan mountain region in western China or eastern Asia (Li & Tamura 2001, Park & al. 2019).

Only one smut fungus, *Urocystis eranthidis* (Pass.) Ainsw. & Sampson, is known to infect plants in *Eranthis*. This fungus is reported from Europe, Asia, North America, and Australia, with all records occurring on yellow-flowered plants: *E. hyemalis, E. cilicica,* and *E. longistipitata* (Ciferri 1938; Ainsworth & Sampson 1950; Fischer 1953; Schwarzman 1960; Vánky 1985, 2011; Scholz & Scholz 1988, 2001, 2013; Denchev 1991, 2001; Azbukina & Karatygin 1995; Scholler 1996; Vánky & Shivas 2008; Beenken & Senn-Irlet 2016; Woods & al. 2018). During an examination of fungal loans from the herbarium of University of Turku, Finland (TUR), an unidentified smut fungus on *Eranthis longistipitata* from Uzbekistan was found. Morphological and molecular studies demonstrated that it represented a new species of *Entyloma* de Bary. Its host belongs to the group of yellow-flowered species of *Eranthis*.

Entyloma is a large genus in the *Entylomataceae,* with 188 recognized species on host plants belonging to 27 families (Vánky 2011; Denchev & al. 2013; Savchenko & al. 2014, 2016; Rossman & al. 2016; Rooney-Latham & al. 2017; Savchenko & Carris 2017; Kruse & al. 2018; Kruse & Thines 2019; Richter & al. 2019). *Entyloma* species form sori in vegetative organs of plants from many different lineages of eudicots, mostly in leaves, rarely in stems, occasionally in roots, usually forming few to numerous spots, sometimes swellings or galls formed by hypertrophic growth of host tissue. The spores are permanently embedded in the host tissue, singly or in irregular groups, hyaline, yellow or yellowish brown, and usually with a smooth, two-layered wall; very rarely the outer layer is tuberculate (e.g., *E. verruculosum*) or torn apart into prismatic, pyramidal or coarse and irregular pieces (e.g., *E. urocystoides*) (Denchev & al. 2013). For many *Entyloma* species, an asexual morph is also recorded (Vánky 2011).

The importance of host specificity in delimiting species within *Entyloma* has varied significantly during the last eight decades. Savile (1947) applied a morphological species concept, based on spore sizes and asexual morph. He synonymized species with similar morphology, parasitizing host species on different genera from the same family. As a result of this broad species concept, Savile accepted only eight species of *Entyloma* on North American asteraceous hosts. Other authors (e.g. Liro 1938, Lindeberg 1959, Vánky 2011) applied narrower species concepts, considering *Entyloma* species as infecting one or more hosts from the same host genus or occasionally a few

Table 1. *Entyloma* species and GenBank accession numbers used for phylogenetic analysis

Species	Host	GenBank # (ITS)	Reference
E. arnicale	*Arnica montana*	AY854964	Boekhout & al. 2006
E. arnoseridis	*Arnoseris minima*	AY081017	Begerow & al. 2002
E. atlanticum	*Geranium tuberosum*	AY081018	Begerow & al. 2002
E. australe	*Physalis cordata*	AY081019	Begerow & al. 2002
E. belangeri	—	AY259074	Richter & al. 2019
E. bidentis	*Bidens pilosa*	AY081020	Begerow & al. 2002
E. browalliae	*Browallia americana*	AY081021	Begerow & al. 2002
E. bullosum	*Ranunculus paludosus*	MF924658	Kruse & al. 2018
E. calceolariae	*Calceolaria chelidonioides*	AY081022	Begerow & al. 2002
E. carmeli	*Eryngium falcatum*	KF310892	Savchenko & al. 2014
E. chrysosplenii	*Chrysosplenium alternifolium*	AY081024	Begerow & al. 2002
E. comaclinii	*Comaclinium montanum*	AY081025	Begerow & al. 2002
E. corydalis	*Corydalis bulbosa*	AY081027	Begerow & al. 2002
E. cosmi	*Cosmos bipinnatus*	KJ728759	Lutz & Piatek 2016
E. costaricense	*Viguiera* sp.	AY081028	Begerow & al. 2002
E. dahliae	*Dahlia* sp.	AY081029	Begerow & al. 2002
E. deliliae	*Delilia biflora*	AY081030	Begerow & al. 2002
E. davenportii	—	AY259064	Richter & al. 2019
E. diastateae	*Diastatea micrantha*	AY081031	Begerow & al. 2002
E. doebbeleri	*Dahlia imperialis*	AY081032	Begerow & al. 2002
E. eburneum	*Ranunculus repens*	MF924689	Kruse & al. 2018
E. elstari	—	AY259048	Richter & al. 2019
E. eranthidis	***Eranthis longistipitata***	**MT118137**	**this study**
E. eryngii	*Eryngium campestre*	AY081033	Begerow & al. 2002
E. eryngii-cretici	*E. creticum*	KF310894	Savchenko & al. 2014
E. eryngii-plani	*E. planum*	AY081034	Begerow & al. 2002
E. ficariae	*Ficaria verna*	MF924702	Kruse & al. 2018
E. fuscum	*Glaucium flavum*	AY081036	Begerow & al. 2002
E. gaillardianum	*Gaillardia aristata*	AY081037	Begerow & al. 2002
E. guaraniticum	*Bidens pilosa*	AY081038	Begerow & al. 2002
E. helianthi	*Helianthus annuus*	KU163607	Rooney-Latham & al. 2017
E. hieracii	*Hieracium sylvaticum*	AY081039	Begerow & al. 2002
E. holwayi	*Cosmos caudatus*	AY081040	Begerow & al. 2002
E. jolantae	*Ranunculus oreophilus*	MF924688	Kruse & al. 2018
E. klenkei	*R. marginatus*	MF924663	Kruse & al. 2018
E. kochmanii	*R. lanuginosus*	MF924678	Kruse & al. 2018

Species	Host	GenBank # (ITS)	Reference
E. lagoeciae	*Lagoecia cuminoides*	MH295129	Kruse & Thines 2019
E. linariae	*Linaria vulgaris*	AY081041	Begerow & al. 2002
E. lobeliae	*Lobelia laxiflora*	AY081042	Begerow & al. 2002
E. madiae	*Madia gracilis*	AY081043	Begerow & al. 2002
E. magocsyanum	*Tordylium cordatum*	KF310891	Savchenko & al. 2016
E. majewskii	*Ficaria verna*	MF924713	Kruse & al. 2018
E. matricariae	*Tripleurospermum perforatum*	AY081044	Begerow & al. 2002
E. microsporum	*Ranunculus repens*	MF924708	Kruse & al. 2018
E. parthenii	*Parthenium hysterophorus*	AY081026	Begerow & al. 2002
E. piepenbringiae	*Ranunculus polyanthemos* subsp. *nemorosus*	MF924664	Kruse & al. 2018
E. polysporum	*Ambrosia artemisiifolia*	AY081046	Begerow & al. 2002
E. randwijkense	—	AY259080	Richter & al. 2019
E. ranunculacearum	*Ranunculus acris*	MF924635	Kruse & al. 2018
E. ranunculi-repentis	*R. repens*	AY081047	Begerow & al. 2002
E. ranunculi-scelerati	*R. sceleratus*	MF924672	Kruse & al. 2018
E. ranunculorum	*R. auricomus*	MF924638	Kruse & al. 2018
E. savchenkoi	*R. paludosus*	MF924675	Kruse & al. 2018
E. scandicis	*Scandix verna*	KF447773	Savchenko & al. 2016
E. serotinum	*Symphytum officinale*	AY081048	Begerow & al. 2002
E. thielii	*Ranunculus montanus*	MF924692	Kruse & al. 2018
E. verruculosum	*R. lanuginosus*	MF924651	Kruse & al. 2018
E. zinniae	*Zinnia peruviana*	AY081049	Begerow & al. 2002

closely related host genera. During the last two decades with the application of molecular methods, it became evident that members of *Entyloma* exhibit a far higher host specificity, parasitizing a single or only a few closely related host species (Begerow & al. 2002, Vánky & Lutz 2010, Savchenko & al. 2014, 2016, Kruse & al. 2018, Kruse & Thines 2019). It also became evident that much higher diversity than currently recognized in *Entyloma* should be expected (Kruse & al. 2018).

From Uzbekistan, 16 different *Entyloma* species are known, among which three are recorded on hosts in *Ranunculaceae:* the *E. ranunculi-repentis* complex on *R. polyanthemos* L., *E. thalictri* J. Schröt. on *Thalictrum minus* L., and *E. winteri* Linh. on *Delphinium biternatum* Huth (Ramazanova & al. 1987, Azbukina & Karatygin 1995).

In the present article, we describe and illustrate a new species of *Entyloma* on *Eranthis* from Uzbekistan, and analyze its phylogenetic affinities in *Entyloma*.

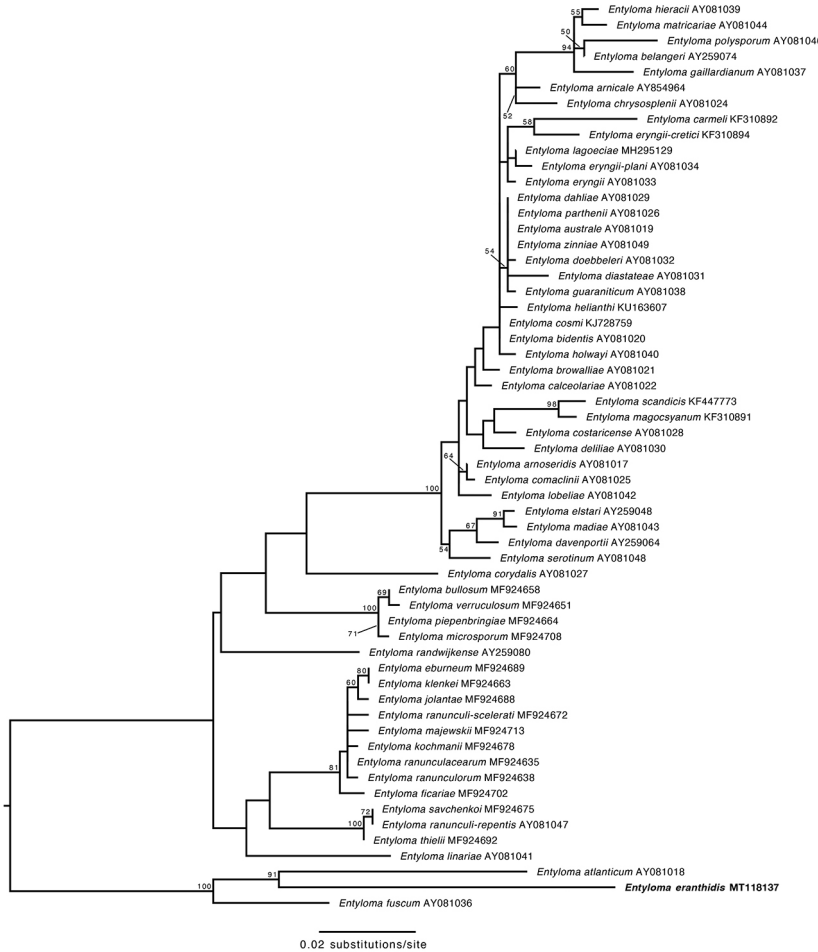

Fig. 1. Phylogenetic relationships of *Entyloma,* based on the RAxML analysis of the complete rDNA internal transcribed spacer (ITS). The new species *Entyloma eranthidis* is depicted in boldface. Bootstrap values of 1000 repetitions ≥50 are shown above branches. The phylogeny was rooted according to Begerow & al. (2002).

Materials & methods

Morphological examination

A dried specimen from the herbarium of University of Turku, Finland (TUR) was examined under light microscope (LM) and scanning electron microscope (SEM). For LM observations and measurements, spores were mounted in lactoglycerol solution

(w : la : gl = 1 : 1 : 2) on glass slides, gently heated to boiling point to rehydrate the spores, and then cooled. The measurements of spores are given as min–max (extreme values) (mean ± 1 standard deviation). For the description of the new species, a total of 300 spores from three sori (100 spores per sorus) were measured. For SEM, spores were attached to specimen holders by double-sided adhesive tape and coated with gold in an ion sputter. The surface structure of spores was observed and photographed at 10 kV accelerating voltage using a Zeiss Sigma VP scanning electron microscope. The description below is based entirely on the specimen examined.

DNA extraction, PCR amplification, and sequencing

Fragments of sori for the smut fungus and leaf tissue for the host plant were removed for DNA extraction. The samples were milled in the Fastprep-24™ Sample Preparation Instrument, using two steel beads. Genomic DNA was isolated using the my-Budget Plant DNA Kit™, according to the manufacturer's protocol 1 ("Isolation of DNA from plant material using lysis buffer SLS"). The rDNA ITS region was amplified using GoTaq™ Master Mix with primer combination ITS1-F/ITS4 (White & al. 1990, Gardes & Bruns 1993) for the smut fungus and ITS1/ITS4 (White & al. 1990) for the host plant. Standard thermal cycling conditions with annealing temperature of 52 °C were used for amplification. Five µl of PCR products were purified using ExoSAP (1:5 diluted in ddH_2O). Amplicons were sequenced in both directions with the BigDye™ Terminator Cycle Sequencing Kit V3.1 on an ABI 3130xl Genetic Analyser at the Faculty of Chemistry and Biochemistry, Ruhr University Bochum, Germany.

Phylogenetic analyses

A multiple sequence alignment of the newly generated *Entyloma* sequence and representative sequences downloaded from NCBIs GenBank (Table 1) was generated using the e-ins-i option in MAFFT v7.450 (Katoh & Standley 2013). Ambiguous positions were removed using GBLOCKS (Castresana 2000) implemented in SEAVIEW (Gouy & al. 2010). A phylogenetic tree was inferred in RAxML 8.2.11 using the GTRGAMMA nucleotide model and a rapid bootstrapping algorithm with 1000 replicates (Stamatakis 2014). The resulting phylogeny was visualized using FigTree v1.4.3 (Rambaut 2012).

Results: Phylogeny and molecular host identification

The phylogenetic analysis of the ITS data produced a topology similar to previous analyses (Begerow & al. 2002), with notable exceptions (Fig. 1). As in Begerow & al. (2002), all species of *Entyloma* on asterids, together with *E. chrysosplenii* and three species known only by their asexual morph, formed a well-supported clade, whereas those on *Ranunculales* were inferred as paraphyletic. Clades within these large groupings sometimes were incongruent with those of Begerow & al. (2002); however we note that in general our phylogeny showed limited statistical support for many clades. Nevertheless, the *Entyloma* species on *Eranthis longistipitata*

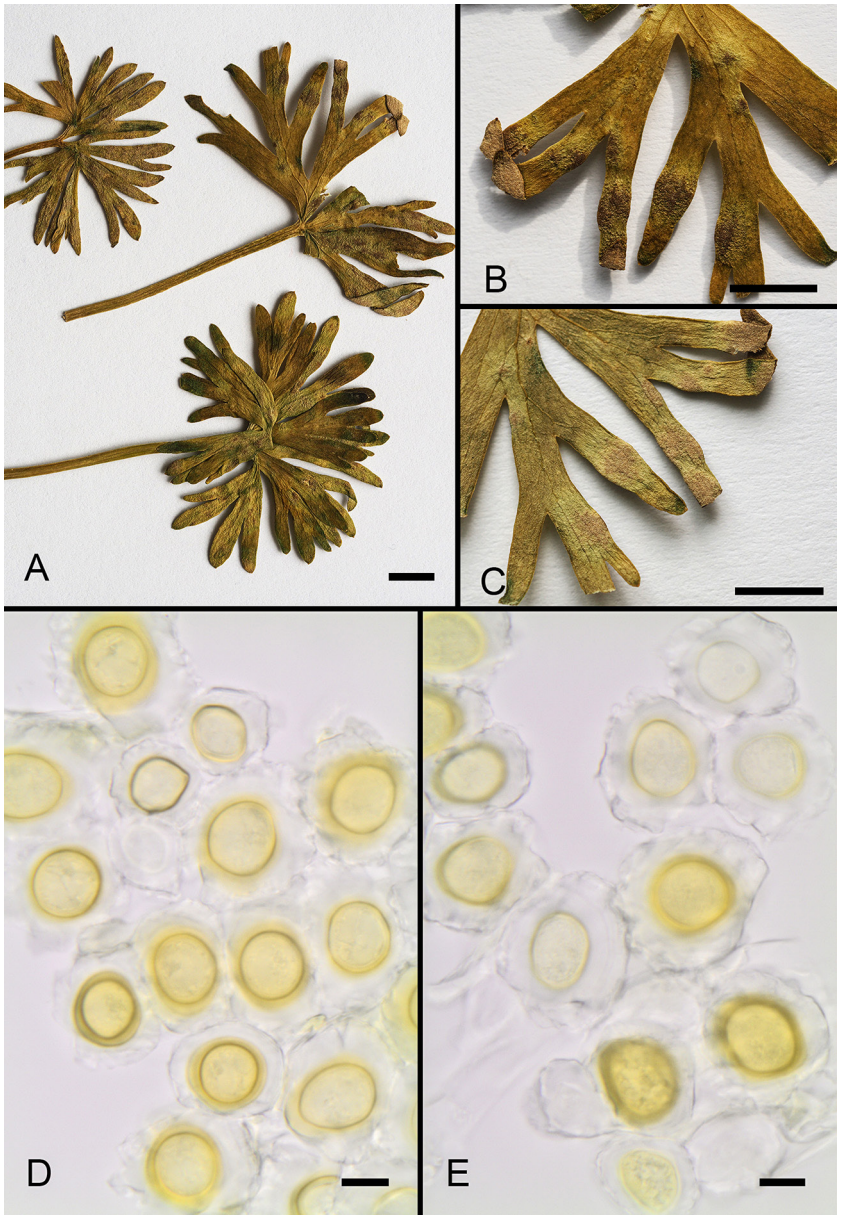

Fig. 2. *Entyloma eranthidis* on *Eranthis longistipitata* (holotype, TUR 109 345): A–C. Habit; D. Spores in LM, median view; E. Spores in LM, surface view. Scale bars: A–C = 0.5 cm; D, E = 10 μm.

formed a statistically well-supported clade with *E. atlanticum* on *Geranium tuberosum* and did not cluster together with other *Entyloma* species on *Ranunculaceae.* This clade was sister group to *E. fuscum* on *Glaucium flavum*.

The identity of the host plant, *Eranthis longistipitata,* was confirmed by ITS sequence data (now deposited in the NCBI with accession no. MT484089). The newly generated ITS sequence had a 99–100% sequence identity and 84% query coverage with the available ITS sequences of *E. longistipitata* in GenBank.

Morphology

The morphology of *Entyloma* is very simple, and differences between the species are consequently very few and vague (Lindeberg 1959). In this genus, the morphological features most commonly used for separating species are: sorus location and characteristics, spore sizes and wall characteristics, and presence of an asexual morph.

The smut fungus on *Eranthis longistipitata* from Uzbekistan is characterized by atypically well-defined morphological features, by which it can be easily distinguished from all species currently recognized in *Entyloma.* With respect to spore size, it produces by far the largest-sized spores in *Entyloma*. The only other *Entyloma* that occasionally has spores exceeding 25 µm, is *E. bullosum* (Sacc.) J. Kruse & al., with spore lengths reaching 21.5(–26.5) µm (Vánky 2011, Kruse & al. 2018). Several "*Entyloma*" species with large "spores" are referred to the *Protomycetales* (Vánky 2011). Although the smut fungus on *Eranthis longistipitata* from Uzbekistan has large spores, the morphological features and ITS sequence data clearly determine its position within *Entyloma.*

A second morphological feature distinguishing this fungus from all currently known *Entyloma* species is its spore wall, which is remarkably thick, (3.5–)4.5–10(–12) µm, with a cracked outer layer. The only other *Entyloma* that has a spore wall reaching 10 µm, is *E. martindalei* (Peck) Piątek, with the inner layer being c. 0.5 µm and the outer layer (1–)2–5 (–9.5) µm thick (Vánky 2011). For the *Entyloma* spp. parasitizing hosts in the *Ranunculales,* thick spore walls with cracked outer layer are not an uncommon morphological feature (e.g., the spore walls of *E. urocystoides* Bubák on *Corydalis solida* (L.) Clairv., *E. bullosum* on *Ranunculus paludosus* Poir., and *E. microsporum* (Unger) J. Schröt. on *Ranunculus* spp.; Denchev 2001, Vánky 2011, Kruse & al. 2018).

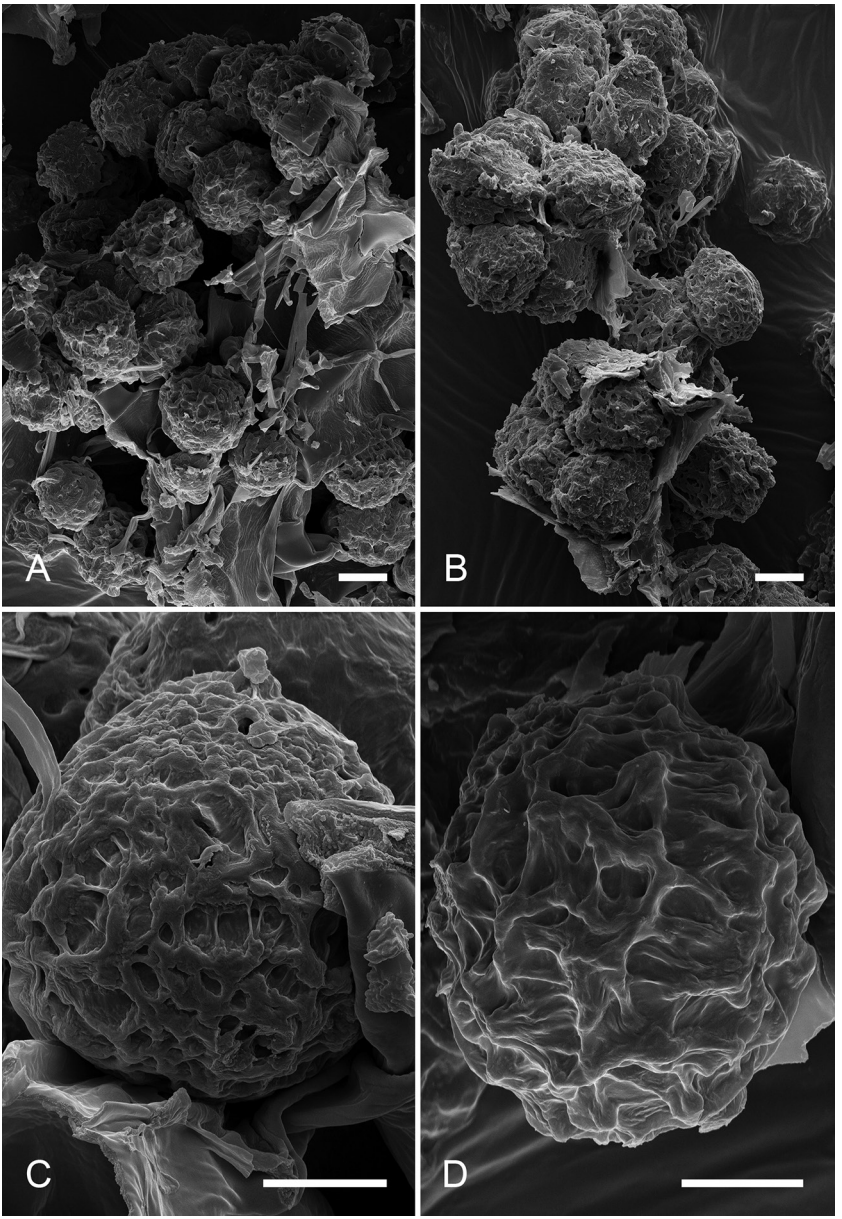

Fig. 3. *Entyloma eranthidis* on *Eranthis longistipitata* (holotype, TUR 109 345). Spores in SEM. Scale bars: A, B = 10 µm; C, D = 5 µm.

Taxonomy

Entyloma eranthidis T. Denchev, Denchev, Kemler & Begerow, **sp. nov.** Figs 2, 3

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Differs from the other *Entyloma* species by specialization on *Eranthis* and by having larger spores and thicker spore walls.

Type—on *Eranthis longistipitata:* Uzbekistan, Tashkent Region, NE of Tashkent, W Tian Shan, Ugamskii Khrebet, NE of Charvak Reservoir, 1100 m, 41°43′N 70°05′E, 1 May 1992, leg. Y. Mäkinen 92–163 (**Holotype,** TUR 109 345).

Etymology—The epithet refers to the host genus.

Sori in leaves, forming irregularly rounded spots, 0.5–2.5 mm long, larger by fusion, amphigenous, not limited by veins, sometimes slightly protruding, reddish brown, peripherally greenish on adaxial side, clay buff on abaxial side of leaves. Spores single, embedded in leaf tissue, usually irregular (because of the cracked surface), variable in size (18–)20–35(–38) × (16.5–)18–28(–31.5) (26.8 ± 3.3 × 23.3 ± 2.8) µm (n = 300), light to medium yellowish brown; spore wall two-layered, (3.5–)4.5–10(–12) µm thick, inner layer yellowish brown, unevenly thickened, (0.8–)1.0–3.5(–4.3) µm thick, outer layer hyaline, highly variable in thickness, (2.5–)3.5–7.5(–9.5) µm thick, initially smooth, at maturity cracking and rupturing irregularly, some ruptures reaching inner layer. As seen by SEM, outer spore wall layer very irregularly ruptured, often forming irregular ridge-like structures. Anamorph not seen.

Comments—The immature spores of *E. eranthidis* are hyaline, with smaller sizes and a thinner, not ruptured, spore wall.

Entyloma eranthidis is known only from the type locality.

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